A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 99: 45–70 (2025)
DOI: 10.3897/neobiota.99.143667

Research Article

Temperature-dependent versatility shapes invasiveness in the tropical freshwater gastropod *Melanoides tuberculata*

Bert Van Bocxlaer[1], Julie Offerle[1], Claudia M. Ortiz Sepulveda[1], Rémi Habert[1], Anne-Catherine Holl[1], Nicolas Denize-Proust[1,2], Alexis Y. Dollion[1,3], Grant Pawindo[4], Fred D. Chibwana[5], Virginie Cuvillier-Hot[1]

1 *CNRS, Univ. Lille, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France*
2 *Institute of Ecology and Environmental Sciences of Paris, UMR 7618, F-75005 Paris, France*
3 *CNRS, Univ. Rennes, Univ. Normandie, UMR 6552 EthoS, F-35000 Rennes, France*
4 *Department of Biological Sciences, Chancellor College, University of Malawi, P.O. Box 280, Zomba, Malawi*
5 *Department of Zoology and Wildlife Conservation, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania*

Corresponding author: Bert Van Bocxlaer (bert.van-bocxlaer@univ-lille.fr)

Abstract

Invasive species cause major losses in biodiversity worldwide and alter ecosystem functioning. Once established, invaders are often impossible to remove from ecosystems, especially in eco-insular systems such as the African Great Lakes. How intrinsic biological properties of invasive taxa interact with human-induced ecosystem modifications is a crucial factor determining invasiveness and our ability to anticipate, prevent and manage bioinvasions. Here we investigate the influence of temperature on key life-history traits, including fecundity, growth, offspring size, survival and parental immune investments, of invasive Asian *Melanoides tuberculata* (Müller, 1774) from Lake Malawi/Nyassa (morph LMI). We subjected populations of this parthenogenetic (clonal) lineage to uniform temperature treatments of 20 °C, 26 °C and 32 °C and monitored adult and juvenile life-history traits. Constitutive (preventative) and infection-induced immune investments of adults were estimated via antibacterial responses to a natural pathogen. Fecundity was low during our experiment and did not differ amongst temperature treatments, but a burst of offspring release occurred in the first two weeks of the experiment. Juvenile size and growth increased with temperature, which resulted in decreasing generation times. Juvenile mortality was, however, elevated at 32 °C. Temperature differences prompted a shift in immune investments. Under cold temperatures, adults invested in costly constitutive immunity, but they did not in warm environments, where strong investments in infection-induced immune responses occurred. This strategy may enable adults in warm environments to redirect energy from immunity to growth and reproduction, therewith, enhancing competitiveness at the cost of reduced offspring survival. We observed contrasting responses in various studied traits, suggesting that *Melanoides tuberculata* adopts compensatory mechanisms to cope with environmental changes. This versatility favours invasiveness and contributes to the competitive pressure which invasive *Melanoides* exerts on native taxa amid global warming and ecosystem change. Understanding the intricate interactions between bioinvasions and environmental change is essential for effective conservation of native species, the stability of their ecosystems and for policy development. Species-specific versatility of invasive species and associated competitive advantages remain understudied, but are critical to predict invasion dynamics in the context of multidimensional anthropogenic stressors, for informed risk assessment and decision-making.

Key words: Eco-immunology, experimental invasion ecology, global warming, invasive species management, life-history traits, red-rim melania, species-specific versatility

OPEN ACCESS

Academic editor: Michael McKinney
Received: 5 December 2024
Accepted: 24 March 2025
Published: 30 May 2025

Citation: Van Bocxlaer B, Offerle J, Ortiz Sepulveda CM, Habert R, Holl A-C, Denize-Proust N, Dollion AY, Pawindo G, Chibwana FD, Cuvillier-Hot V (2025) Temperature-dependent versatility shapes invasiveness in the tropical freshwater gastropod *Melanoides tuberculata*. NeoBiota 99: 45–70. https://doi.org/10.3897/neobiota.99.143667

Copyright: © Bert Van Bocxlaer et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Human-induced global changes in land use, resource extraction, bio-invasions and climate cause major losses in biodiversity and pervasive alterations of ecosystem functioning. How various changes interact with one another represents one of the largest uncertainties in projections of future biodiversity change (Sala et al. 2000; Weiskopf et al. 2020) and a challenge for sustainable biological resource management (McNeely et al. 2001; IPBES 2019; CBD 2020). Biotic exchange is a pervasive stressor in freshwater ecosystems and especially in eco-insular lakes because of their discontinuous nature (Sala et al. 2000; Dudgeon et al. 2006; Hecky et al. 2010; Tickner et al. 2020). The arrival and establishment of invasive species is often facilitated by other anthropogenic stressors, such as land use, overfishing and climate change, which hasten ecosystem deterioration and may vacate previously occupied niches (Strayer 2010; Donohue et al. 2013). Once established, invasive species are difficult to remove from an ecosystem (Rader et al. 2003) and, although they may initially enhance local or regional biodiversity or generate evolutionary novelties, they ultimately have complex adverse effects on local biodiversity and ecosystem functioning (Pejchar and Mooney 2009) up to provoking fundamental ecosystem shifts (Scheffer et al. 2001).

The drivers of global change are often complex and multi-layered. Changes in ambient temperatures may affect species richness and community structure (Mayhew et al. 2012; Antão et al. 2020), geographic range (Lenoir and Svenning 2015), abundance (Szuwalski et al. 2023), sex ratio (Jensen et al. 2018), body size, fitness, metabolic rates and behaviour (Sponaugle et al. 2006; Angilletta 2009; Dillon et al. 2010; Ciota et al. 2014) amongst others. Furthermore, temperature changes may have differential effects amongst sexes, populations and species (De Block and Stoks 2003; Wang et al. 2020; Gissi et al. 2023). Likewise, invasive species may have direct and indirect effects on ecosystems and species-interactions, with impacts depending on their intrinsic biological properties compared to those of native taxa (Lodge 1993; Pejchar and Mooney 2009).

Many invasive species share traits, for example, dispersal ability, growth rate and generation time, enabling them to capitalise on various aspects of global change (Lodge 1993; Dukes and Mooney 1999; Whitney and Gabler 2008; Hulme 2017). They often have uniparental reproduction, tolerate a wide range of physico-chemical conditions and may have high capabilities for ecophenotypic plasticity and/or rapid evolutionary adaptation, all of which may facilitate colonisation of new environments (Whitney and Gabler 2008; Huang et al. 2017). In this context, the refined hypothesis of 'evolution of increased competitive ability' (EICA-refined hypothesis) proposes that invasive capacities rely on coping with new immune threats by rapidly shifting to less costly, more targeted immune strategies in non-native areas (Lee and Klasing 2004; Cornet et al. 2016; Prüter et al. 2020). Resources not allocated to immune defence can instead be redirected towards growth, reproduction and/or dispersal. Experimental support for this hypothesis is limited and further research is required to better understand physiological factors that affect invasiveness, which would aid predictions of future species introductions and associated ecosystem impacts (Hulme 2017).

As climate change may affect invasiveness, we examined how temperature influences life-history traits and immune status in the invasive freshwater gastropod *Melanoides tuberculata* (Müller, 1774), leveraging an experiment with morph LMI

from Lake Malawi/Nyassa. *Melanoides tuberculata*, in its current taxonomic identity, is considered native to tropical and subtropical Asia, Africa and Oceania (Brown 1994; Genner et al. 2004), but it includes several deeply divergent lineages and is to be revised (Genner et al. 2007; Van Bocxlaer et al. 2015; Tolley-Jordan et al. 2023). Since the 1970s, several lineages from Southeast Asia have been introduced in Africa and America and have since become widespread throughout tropical and subtropical freshwater environments, including on various oceanic islands (Facon et al. 2003; Genner et al. 2004; Van Bocxlaer et al. 2015). Additional invasions are reported from more temperate regions, in Europe and New Zealand amongst others, especially from hot springs and thermal effluents (Duggan 2002; Oscoz et al. 2010), indicating a strong global propagule pressure and frequent accidental introductions, likely via aquarium trade (Facon et al. 2008; Van Bocxlaer et al. 2015). *Melanoides tuberculata* primarily affects benthic fauna (Rader et al. 2003; Van Bocxlaer and Albrecht 2015) and has been deliberately introduced in American waterbodies for controlling intermediate snail hosts of trematodes that cause schistosomiasis (Pointier 2001), although it can host other trematodes (Rader et al. 2003; Ben-Ami and Heller 2005). It is uncertain how *M. tuberculata* will spread further throughout freshwater ecosystems globally, how its presence affects native taxa, human and animal health and how effects will resonate through ecosystems.

Here, we aim to better understand how *Melanoides tuberculata* capitalises on rapid environmental change and how temperature will affect its future invasion potential. Various hypotheses exist on temperature-related changes in life-history traits. Higher temperatures may accelerate development, but may also increase mortality (see Ciota et al. (2014)). Higher survivorship in colder environments and large geographic ranges may induce intraspecific variation in ectotherms consistent with Bergmann's rule, thus that growth is slower and maturation occurs at larger body size at lower temperatures (Atkinson 1994; Angilletta et al. 2004; Angilletta 2009). This hypothesis contrasts with expectations from optimality models that maturity should be reached at smaller size in environments where growth is retarded (Stearns and Koella 1986; Berrigan and Charnov 1994). Extreme temperatures may cause stress and reduced immune defences, resulting in a lower resistance to pathogens, as in various marine molluscs facing global warming (Li et al. 2007; Travers et al. 2009; Dang et al. 2012). Organisms use various defence mechanisms, including constitutive (preventative) defences, which are constantly active and energy-intensive and infection-induced defences, which are activated only upon infection, reducing energetic costs (Schmid-Hempel and Ebert 2003). According to the EICA-refined hypothesis, adjusting immune investments, based on environmental conditions and pathogen risks, may enhance fitness (Schmid-Hempel and Ebert 2003; Kamiya et al. 2016; Boots and Best 2018) and could benefit invasive species facing sudden immune changes upon colonisation of new regions (Torchin et al. 2003; Lee and Klasing 2004). To test these hypotheses, we examined how low, medium and high temperatures affect life-history traits and immune investments in *M. tuberculata* at the population scale. We expected intermediate temperatures to yield higher offspring production than low and high temperatures due to reduced physiological stress and that growth would increase with metabolic rates and, thus, temperature. For immunity, we anticipated that extreme temperatures would result in decreased defence strategies, but we were uncertain about whether *M. tuberculata* regulates life-history strategies and immune defences and how versatility may contribute to invasiveness.

Materials and methods

Study system

Melanoides tuberculata inhabits all types of freshwater habitats, except for ephemeral pools, lives endobenthically in sandy or silty substrates and feeds mainly at night on benthic microalgae, fine detritus, epiphytic algae and decaying plants (Lévêque et al. 1983; Madsen 1992; Brown 1994). It is eurytopic as to salinity, concentrations of dissolved oxygen and has a temperature range of ~ 18–32 °C (Mitchell and Brandt 2005). The species usually reproduces through obligate apomixis with ova being produced via mitosis, but some populations reproduce sexually (Jacob 1957; Livshits and Fishelson 1983; Heller and Farstey 1990). Adult females have a large brood pouch, located dorsal to the head and foot, which may contain up to ~ 70 juveniles (Berry and Haji Kadri 1974; Livshits and Fishelson 1983; Ben-Ami and Hodgson 2005). *Melanoides tuberculata* grows slowly, with an onset of reproduction ~ 140–180 days after being released from their mother (Livshits and Fishelson 1983; Pointier et al. 1992), although larger variation has been reported (Dudgeon 1986; Okumura and Rocha 2020), which may relate to differences in life-history traits amongst the divergent lineages of this nominal species. The species has a life span of up to five years in the wild (Pointier et al. 1992; Ben-Ami and Hodgson 2005).

We conducted our experiment with morph LMI of *M. tuberculata* collected from the southern region of Lake Malawi/Nyassa in 2010, where it has been observed at population densities of up to 5140 individuals/m^2 (Genner et al. 2004; Van Bocxlaer and Albrecht 2015). This morph belongs to the invasive Malawi-Congo clade (see Van Bocxlaer et al. (2015)), which corresponds to clade 1 of *M. tuberculata* in Tolley-Jordan et al. (2023). Morph LMI has presumably colonised Lake Malawi/Nyassa in the 1980s or 1990s (Genner et al. 2004) and is closely related to specimens retrieved from Singapore and Lombok, Indonesia. Representatives of this clade have also colonised various parts of the Congo River near Kisangani and Kinshasa in the DR Congo, Eseka in Cameroon, Tumbes in Peru, the Misiones Province of Argentina and Florida in the USA (Van Bocxlaer et al. 2015). Genetically, they are divergent from native African *M. tuberculata* and from other oriental lineages that have colonised Burundi (Van Bocxlaer et al. 2015) and Martinique (Facon et al. 2003).

During the ~ 11 years prior to this experiment, our laboratory population of morph LMI of *M. tuberculata* was kept in a single 60 litre aquarium at 25–26 °C, pH ~ 7.5–8.0, with a substrate of sand, coral sand and chicken eggshell, initially under natural light, but later, under LED light with a photoperiod of ~ 8 h/day. The population was fed *ad libitum* with Novo Pleco pellets (JBL, Neuhofen/Pfalz, Germany). Our laboratory population has reproduced exclusively via apomictic parthenogenesis since 2010, so all individuals are female and share a quasi-identical genotype. As we maintained the population for multiple generations under controlled laboratory conditions and, given the homogeneous genetic background, all individuals displayed similar life-history traits, infection status and immune strategies at the start of the experiment.

Experimental design

We conducted our experiment with three temperature treatments: low (LT, ~ 20 °C), medium (MT, ~ 26 °C) and high (HT, ~ 32 °C), based on the tolerance limits of *M. tuberculata* and three replicates per treatment, resulting in nine

aquaria, each measuring 19.0 × 14.5 × 19.0 cm (l × w × h), with a volume of ~ 5,200 cm^3. Each aquarium was filled with 4 litres of a mix of 50% tap water and 50% osmotic water and water levels were kept constant by adding osmotic water to offset evaporation. No substrate was added, which facilitated the detection of new offspring and cleaning, therewith reducing risks of haphazard pathogen infections. The temperature in each aquarium was controlled by a submersible thermostatic heater (Eheim, Thermocontrol 50 W) and the water was oxygenated (Eheim Air Pump 200; one pump per replicate set). We monitored temperature, pH and conductivity biweekly with a Combo HI98129 probe (Hanna Instruments). Weekly, aquaria were cleaned and 50–80% of the water was changed (the exact volume depending on how soiled aquaria were, but always the same volume for all aquaria).

Each aquarium was populated with 10 F_0 adults that were randomly selected from our laboratory stock on 02/04/2021, reflecting a density of ~ 350 snails/m^2, which is low to moderate compared to the population densities observed in Lake Malawi/Nyassa (see above). Upon creating experimental populations, 10 individuals from the laboratory stock were flash-frozen in liquid nitrogen and conserved at -80 °C to document immune status at the onset of our experiment (F_0 at T_0). Each population was fed daily with 20 mg of Novo Pleco pellets. All F_1 juveniles released during the same week were considered to represent a single 'cohort'. Weekly, we collected and counted juveniles, took pictures and marked them with distinct colours per cohort using water-based acrylic paint (Posca). This cohort-specific colour coding and shell features, notably the geometric pattern of orange-red spots/flames on the shell, allowed us to document growth individually. We followed the first six cohorts in detail, but after 6.5 weeks (on 17/05/2021), we sacrificed five F_0 adults per aquarium to assess their immune status (see below). Initially, we had planned to sacrifice all F_0 adults simultaneously, but limited reproduction and substantial juvenile mortality in some treatments required us to alter this strategy. Therefore, the remaining five F_0 adults and all F_1 juveniles were left to develop offspring populations in each aquarium under the same conditions as indicated before. After nine months (on 05/01/2022), before the F_1 offspring became reproductively active, the other five F_0 adults per aquarium were sacrificed to assess immune status, therewith allowing assessment of the onset of reproduction in F_1 offspring. We observed no adult mortality during the first 6.5 weeks of the experiment, so that all life-history trait data are directly comparable, but seven adults died between 17/05/2021 and 05/01/2022 and were excluded from subsequent immune status examinations.

As the number of developing young in the brood pouch of *M. tuberculata* has been reported to increase with shell height (Berry and Haji Kadri 1974; Dudgeon 1986; Pointier et al. 1992), we expected fecundity and/or juvenile size to correlate with female body size. Therefore, we verified that our initial populations were homogeneous in shell height to avoid bias. Adults were pictured in apertural view at the onset of the experiment (02/04/2021) and after 6.5 weeks (17/05/2021), using a Canon Eos 700D DSLR camera with EFS 60 mm macro lens. Adult size was measured from these pictures using ImageJ v.2.1.0 (Schneider et al. 2012).

Documentation of life-history traits

Weekly, juveniles were collected from each aquarium, assigned to their cohorts and photographed using a Zeiss Stemi 305 binocular (zoom ×8) with an Axiocam 105 camera. During this procedure, we counted and (re-)coloured individuals,

documented mortality and removed deceased juveniles from the experimental populations. Juvenile size was measured with ImageJ at birth and individual growth was documented over two-week periods. Juvenile mortality was calculated as the percentage of dead juveniles between the day the cohort was harvested and the end of the experiment, providing insight into survival.

Immune status assessments

Molluscs produce antimicrobial compounds (e.g. lysozymal enzymes, lectins, antimicrobial peptides) to prevent and repel infections. Infection-induced defences activate upon microbial detection via pattern-recognition immune receptors (Li et al. 2023). We assessed the immune investments of adult snails by measuring their ability to kill or inhibit growth of *Bacillus cereus*, a common molluscan pathogen isolated from the stock aquaria prior to the experiment and found in African lakes (see Suppl. material 1). We quantified individual immune investments by comparing the growth rate of *B. cereus* aliquoted from a fresh bacterial culture in the presence of standardised *M. tuberculata* samples. In our experiment, such resistance tests provide measures of immunocompetence, with lower bacterial growth rates indicating higher immune investments.

The five adult *M. tuberculata* per population sacrificed after 6.5 weeks (17/05/2021) were used to assess constitutive immune levels (i.e. without bacterial stimulation), whereas those sacrificed on 05/01/2022 were used to assess total immune responses after bacterial stimulation. These total immune responses represent the sum of constitutive and infection-induced responses. Bacterial stimulation was performed by pricking the foot with a needle that was previously dipped in a solution of dead *B. cereus*, allowing us to measure individual immune responses without interference from bacterial growth dynamics (see Suppl. material 1). Immune-challenged snails were incubated for three hours in their experimental conditions before flash-freezing in liquid nitrogen. Sacrificed snails were individually homogenised in liquid nitrogen using pestle and mortar. The resulting powder was re-suspended in 50–150 µl of filtered phosphate-buffered saline (PBS), vortexed and then centrifuged for 10 minutes (10,000 rpm, 4 °C). One microlitre of the obtained supernatant was used to quantify the total protein content via a Bradford (1976) assay (PanReac AppliChem).

Antibacterial tests followed a protocol adapted from Pinzón et al. (2014) and are fully described in Suppl. material 1. Tests were run in sterile 96-well microplates, with each sample standardised on total protein content in filtered PBS to a final volume of 20 µl, including negative and positive controls (see Suppl. material 1). We used a single *B. cereus* culture per immune investment strategy, adding 180 µl of the bacterial culture to each sample. Bacterial growth rates were reconstructed from growth curves established from consecutive absorbance readings every 10 minutes during a 6-hour period on an Infinite 200Pro spectrophotometer (Tecan), considering only the exponential growth phase.

Statistical analysis

Statistical analyses of life-history traits and immune status were performed in a nested design with tests amongst populations, treatments and replicates. The input data for these tests were either population-level summary statistics (e.g. for fertility) or individual measurement data (e.g. for size and growth).

Individual measurements lead to a potential risk of pseudoreplication, because measurements on several individuals belonging to the same population are not truly independent. Our nested statistical design allows us to correctly estimate treatment effects, while considering population-to-population variability. We used two statistical approaches, which gave highly congruent results. First, we used nested non-parametric Kruskal-Wallis tests followed by pairwise Dunn's tests with false discovery rate correction (Benjamini and Hochberg 1995), because normality was often rejected for some populations with Shapiro-Wilk tests (for continuous data) or poorly approximated with discrete data upon visual inspection. These tests were implemented with functions from dunn.test v.1.3.5 (Dinno 2017) and multcompView v.0.1-8 (Graves et al. 2019). Second, when individual measurement data were available, we additionally used linear mixed models with treatment (n = 3) as fixed effect and population (n = 9) as random effect. As mentioned, normality was regularly rejected for some populations, but a Gamma distribution was usually not (except for data on juvenile size in LT1, see below), so we fitted generalised linear mixed models (glmm) with Gamma distributions, either to untransformed data or with a logarithmic link function. To assess whether including populations as random effect was justified, we also developed a generalised linear model (glm) that only differed from the glmm by the absence of a random effect and compared model support of both models using an Akaike Information Criterion (AIC). In all cases, the glm had a lower AIC score than the glmm or the ΔAIC was small (< 3), leading us to retain the simpler glm. We further evaluated retained glms by simulating residuals to test model assumptions of linearity, normality of the residuals, dispersion and homogeneity of the variances. We only found critical violations in one model (on total immune responses), which were resolved by further simplifying the model using a Gaussian rather than a Gamma distribution. These analyses were conducted using the R packages goft v. 1.3.6 (González-Estrada and Villaseñor-Alva 2020), glmmTMB v. 1.1.10 (Brooks et al. 2017) and DHARMa v. 0.4.7 (Hartig 2024). Post-hoc pairwise comparisons were performed with false discovery rate correction using emmeans v. 1.10.7 (Lenth 2025). All statistical analyses were performed in R v.4.1.2 (R Core Team 2021).

Results

Experimental conditions

Experimental conditions were stable during the experiment, with no differences in pH amongst aquaria, treatments and replicates (Suppl. material 1: fig. S1A; Kruskal-Wallis tests; aquaria: $\chi^2 = 4.36$; df = 8; $p = 0.823$; treatments: $\chi^2 = 1.89$; df = 2; $p = 0.389$; replicates: $\chi^2 = 1.43$; df = 2; $p = 0.490$). We found small, but significant differences in conductivity amongst aquaria, treatments and replicates (Suppl. material 1: fig. S1B; Kruskal-Wallis tests; aquaria: $\chi^2 = 29.89$; df = 8; $p < 0.001$; treatments: $\chi^2 = 13.36$; df = 2; $p = 0.001$; replicates: $\chi^2 = 9.69$; df = 2; $p = 0.008$). These differences were driven by aquaria MT2 and HT2, which had a ΔCond of 25 and 40 µS/cm above the median of other aquaria, respectively (total standard deviation = ~ 25 µS/cm). As expected, highly significant differences were observed in temperature amongst aquaria and treatments, but not amongst replicates (Suppl. material 1: fig. S1C; Kruskal-Wallis tests; aquaria: $\chi^2 = 330.07$; df = 8; $p < 0.001$; treatments: $\chi^2 = 296.12$; df = 2; $p < 0.001$; replicates: $\chi^2 = 1.04$; df = 2; $p = 0.593$).

Parent size and growth

Upon verifying shell length of parents, normality was rejected for one parent population (Shapiro-Wilk tests; HT3: $W = 0.798$; $p = 0.0138$), but a Gamma distribution was not rejected for any population. We found no significant differences in shell length amongst populations, treatments and replicates (Fig. 1A; Kruskal-Wallis tests; populations: $\chi^2 = 5.43$, df = 8, $p = 0.711$; treatments: $\chi^2 = 0.50$, df = 2, $p = 0.779$; replicates: $\chi^2 = 2.31$, df = 2, $p = 0.315$), which was also confirmed by our glm (see Suppl. material 1). Parental growth over 6.5 weeks was limited, but on average 2 × larger in HT populations than in LT populations, although the variance increased with temperature (mean ± sd: LT = 0.14 ± 0.08 mm; MT = 0.21 ± 0.14 mm; HT = 0.31 ± 0.20 mm; Fig. 1B). Whereas normality was rejected for adult growth in some populations (Shapiro-Wilk tests; LT2: $W = 0.798$; $p = 0.014$; MT3: $W = 0.823$; $p = 0.027$), a Gamma distribution was not. Growth differences were significant amongst populations and amongst treatments, but not amongst replicates (Fig. 1B; Kruskal-Wallis tests; populations: $\chi^2 = 17.87$; df = 8; $p = 0.022$; treatments: $\chi^2 = 12.54$; df = 2; $p = 0.002$; replicates: $\chi^2 = 1.64$; df = 2; $p = 0.440$). Dunn's tests indicated limited statistical power for pairwise population comparisons, but significant differences existed between LT and HT treatments ($Z = -3.541$, $p < 0.001$) and between LT and MT ($Z = -1.752$, $p = 0.040$), whereas differences between HT and MT were trending towards significance ($Z = 1.789$, $p = 0.055$). Post-hoc pairwise comparisons amongst treatments with our glm (see Suppl. material 1) were highly similar to the results of the Dunn's tests, except that the difference between HT and MT was also significant (df = 87, *t*-ratio = 2.420, $p = 0.022$).

Measurements of life-history traits

As to fecundity, in total, 167 individuals were born in the first six weeks of the experiment. Per aquarium, on average 3.09 ± 3.38 (mean ± sd) juveniles emerged per cohort (range: 0–15; Fig. 2A). We found no significant differences in fecundity amongst populations, nor treatments, nor replicates (Kruskal-Wallis tests; populations: $\chi^2 = 8.65$, df = 8, $p = 0.372$; treatments: $\chi^2 = 0.57$, df = 2, $p = 0.753$; replicates: $\chi^2 = 5.70$, df = 2, $p = 0.058$). There was a highly significant difference in the number of juveniles produced throughout the various cohorts (Kruskal-Wallis test; $\chi^2 = 19.17$, df = 5, $p = 0.002$), which was driven by a significantly larger number of individuals produced in cohort 1 than in other cohorts regardless the treatment (Fig. 2B).

The size of juveniles at birth was 2.17 ± 0.60 mm, 2.61 ± 0.94 mm and 2.64 ± 0.71 mm for LT, MT and HT populations, respectively. Size data were not normally distributed for some populations (Shapiro-Wilk tests; LT1: $W = 0.88$, $p = 0.011$; HT3: $W = 0.88$, $p = 0.012$), but the fit to a Gamma distribution was not rejected, except for LT1 (Gamma tests; $V = -3.778$, $p = 0.008$). Highly significant differences in juvenile sizes were observed amongst populations and treatments, but not amongst replicates (Fig. 3A; Kruskal-Wallis tests; populations: $\chi^2 = 31.10$, df = 8, $p < 0.001$; treatments: $\chi^2 = 14.27$, df = 2, $p < 0.001$; replicates: $\chi^2 = 3.87$, df = 2, $p = 0.145$). These results were driven by highly significant size differences between LT and HT treatments ($Z = -3.641$, $p < 0.001$) and significant differences between LT and MT treatments ($Z = -2.686$,

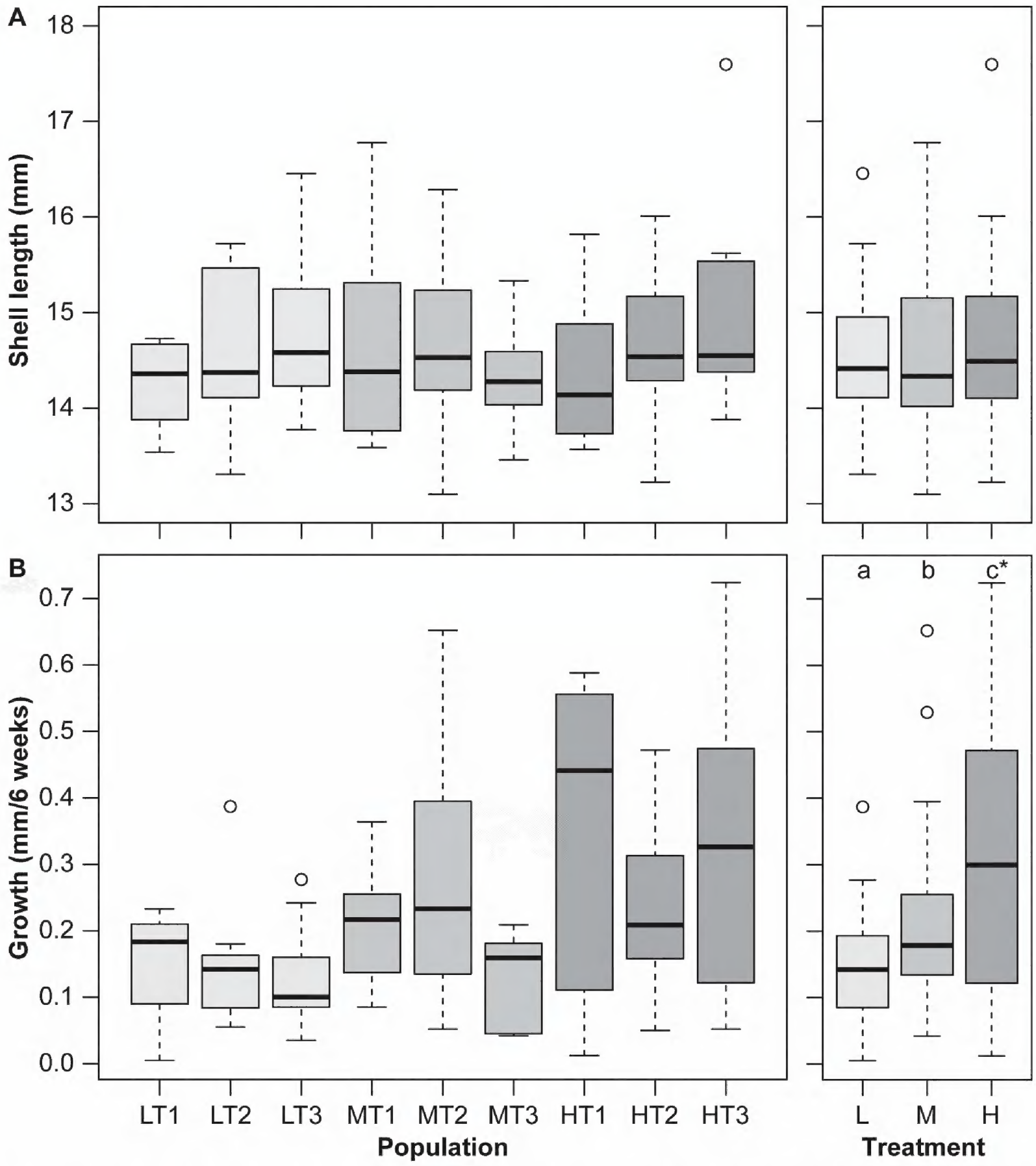

Figure 1. Parent shell length at the start of the experiment **A** and growth throughout the first 6.5 weeks **B** for populations (left) and treatments (right). Greyscale colours indicate treatment conditions, i.e. low, medium and high temperatures from light to darker. Significant differences are indicated by different letters above the box plots (letters are absent when no significant differences were found throughout the panel). The asterisk indicates a slight difference in outcome between statistical tests: the difference between the MT and HT treatments is significant in post-hoc testing for the glm, whereas trending to significance in pairwise comparisons following our Kruskal-Wallis test.

$p = 0.005$), but not between HT and MT treatments ($Z = 0.995$, $p = 0.160$), as confirmed by our glm (see Suppl. material 1). We found no significant differences in the size of juveniles amongst cohorts (Kruskal-Wallis test; $\chi^2 = 7.09$, df = 6, $p = 0.313$), nor significant interactions between treatments, replicates and cohorts (glm with Gamma distribution and logarithmic link).

We observed that juveniles in high temperature populations grew on average ~ 2 × and ~ 4 × faster than those in medium and low temperature populations, respectively (mean ± sd: LT: 0.08 ± 0.07 mm/2 weeks; MT: 0.14 ± 0.09 mm/2 weeks; HT: 0.30 ± 0.23 mm/2 weeks). Juvenile growth data was not normally distributed for several populations (Shapiro-Wilk tests; LT3: $W = 0.814$, $p = 0.030$; MT2: $W = 0.838$, $p = 0.0265$; HT3: $W = 0.800$, $p = 0.010$), but a Gamma distribution

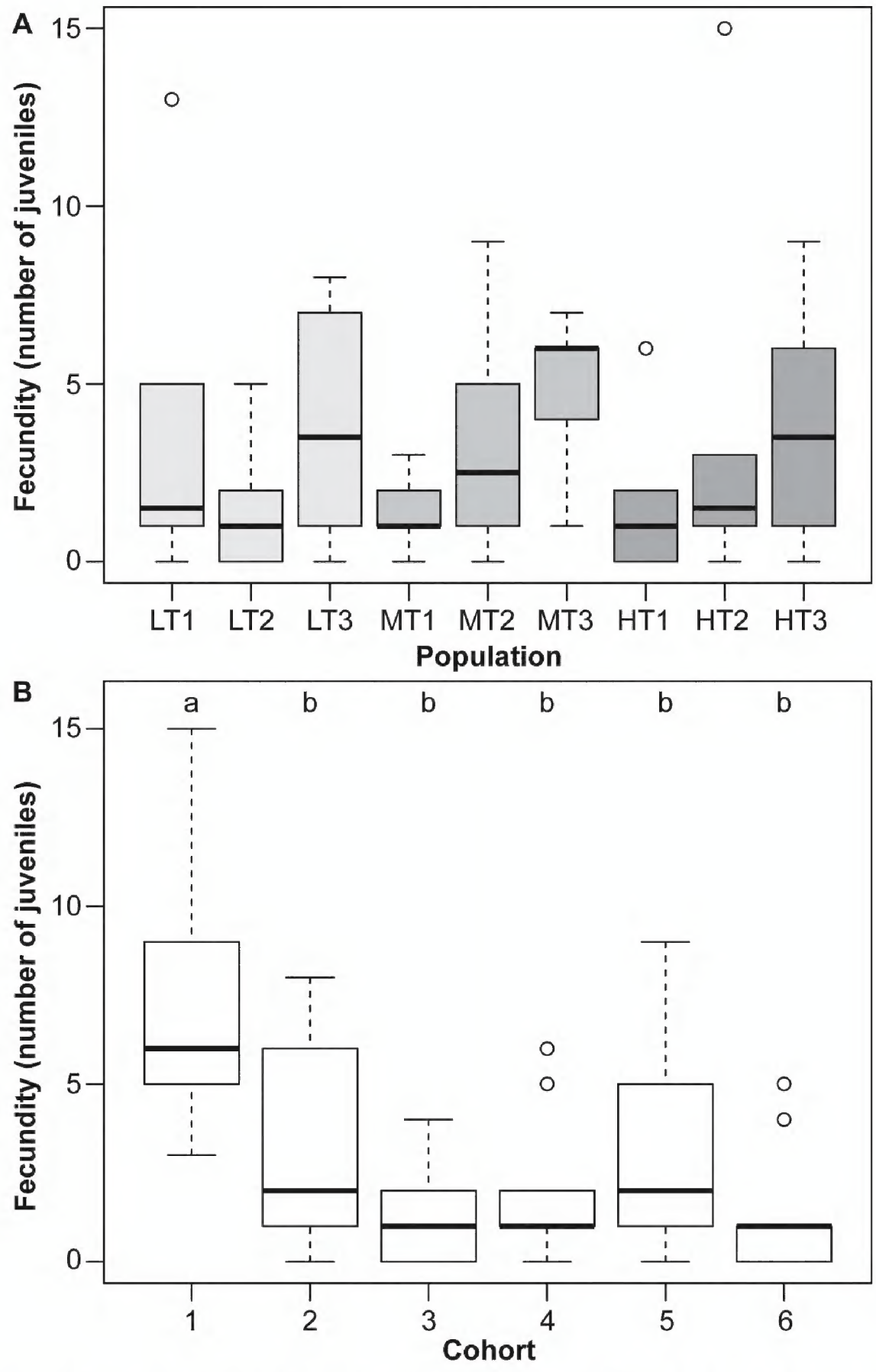

Figure 2. Weekly fecundity within the various populations **A** and amongst cohorts **B** across populations. Significant differences are indicated by different letters above the box plots (letters are absent when no significant differences were found throughout the panel).

was not rejected for any population. Overall, differences in juvenile growth were highly significant amongst populations and amongst treatments, but not amongst replicates (Fig. 3B; Kruskal-Wallis tests; populations: $\chi^2 = 32.90$, df = 8, $p < 0.001$; treatments: $\chi^2 = 28.72$, df = 2, $p < 0.001$; replicates: $\chi^2 = 5.38$, df = 2, $p = 0.068$). Differences are highly significant between LT and HT ($Z = -5.342$, $p < 0.001$) and significant between LT and MT ($Z = -2.9332$, $p = 0.003$) and between HT and MT ($Z = 2.530$, $p = 0.006$); all of these results were confirmed by our glm (see Suppl. material 1). No significant differences were observed in growth rates among cohorts (Kruskal-Wallis test; $\chi^2 = 6.49$, df = 2, $p = 0.261$).

We did not observe mortality in adults during the first 6.5 weeks of the experiment, but per population on average 59.60 ± 35.93% of juveniles died over this period. Significant differences in mortality were observed amongst treatments, but not amongst populations nor replicates (Kruskal-Wallis tests; populations: $\chi^2 = 10.22$, df = 8, $p = 0.250$; treatments: $\chi^2 = 6.43$, df = 2, $p = 0.040$; replicates:

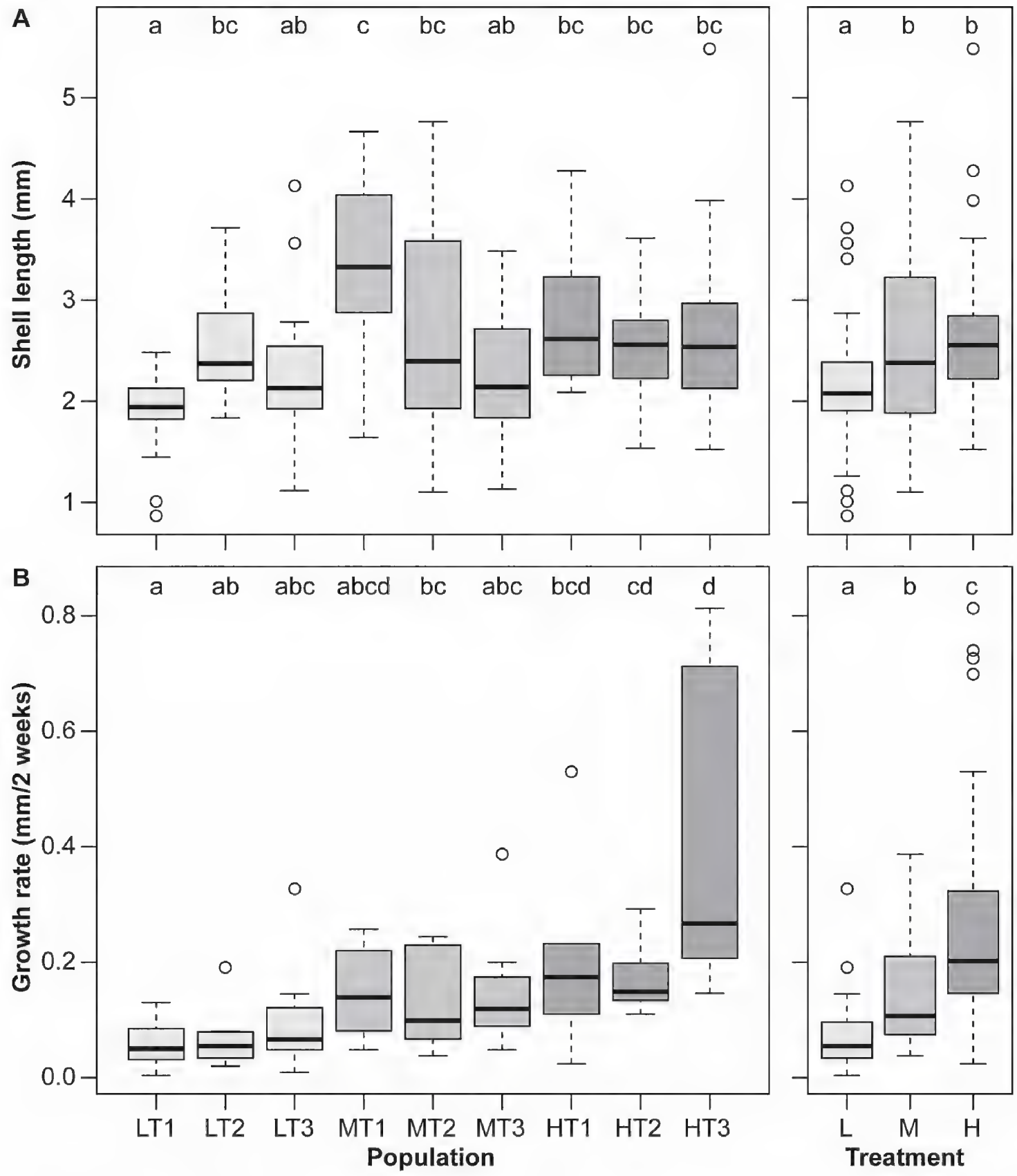

Figure 3. The shell length of juveniles at birth **A** and their growth rate **B** for populations and treatments. Significant differences are indicated with different letters above the box plots.

χ^2 = 1.60, df = 2, p = 0.448). Mortality was higher in HT versus LT (Z = 2.397, p = 0.025) and in HT versus MT populations (Z = 1.935, p = 0.040), whereas there was no significant difference between LT and MT populations (Z = -0.510, p = 0.305). High juvenile mortality prevented us from measuring generation times precisely, but they were ~ 5, ~ 7 and ~ 9–10 months in HT, MT and LT populations, respectively (The duration of our experiment was longer than the generation time in the HT and MT treatments due to high juvenile mortality in early cohorts). Generation time was defined as the period between release of an F_1 individual from the mother's brood pouch and emergence of its first F_2 juvenile.

Immune status

As to constitutive immune responses, normality was rejected for HT1 (W = 0.764, p = 0.040), but a Gamma distribution was not rejected for any population. We observed highly significant differences in constitutive immune defences amongst populations and treatments, but not amongst replicates (Fig. 4A; Kruskal-Wallis tests; populations:

χ^2 = 33.56; df = 10; p < 0.001; treatments: χ^2 = 27.83; df = 4; p < 0.001; replicates: χ^2 = 2.77; df = 2; p = 0.251). Individuals in LT and MT treatments displayed highly significantly larger constitutive immune investments than those in HT (HT – LT: Z = 4.175, p < 0.001; HT – MT: Z = 3.607, p < 0.001; LT – MT: Z = -0.631, p = 0.293), which was also confirmed by our glm (see Suppl. material 1). These differences are evidenced by a ~ 15% reduction in *B. cereus* growth in LT and MT versus HT treatments. Constitutive immune defences were also higher in LT and MT treatments compared to the initial t_0 conditions at the start of the experiment (LT – t_0: Z = -2.485, p = 0.013; MT – t_0: Z = -1.962, p = 0.042). A slight, non-significant decrease in bacterial growth was observed for the t_0 individuals compared to our positive control samples (bacteria + saline), but not in HT individuals.

Normality was rejected for total immune responses after bacterial stimulation in several populations (LT1: W = 0.717, p = 0.014; HT2: W = 0.745, p = 0.027; HT3: W = 0.552, p < 0.001), but a Gamma distribution was not rejected for any population. Total immune responses consist of constitutive and infection-induced responses and we observed highly significant differences amongst populations and treatments, but also significant differences amongst replicates (Fig. 4B; Kruskal-Wallis test; populations: χ^2 = 36.24; df = 8; p < 0.001; treatments: χ^2 = 27.18; df = 3; p < 0.001; replicates: χ^2 = 13.26; df = 2; p = 0.001). Differences amongst replicates result from an overall increase in variance within treatments compared to constitutive immune responses (Fligner-Killeen test of homogeneity of variances: χ^2 = 35.84; df = 1; p < 0.001). All treatments display significant differences in total immune defences after bacterial stimulation compared to our positive control, with mean reductions of ~ 33%, ~ 47% and ~ 73% in bacterial growth in LT, MT and HT individuals, respectively. Furthermore, there are significant differences between HT and LT treatments (Z = -2.27, p = 0.017), differences that trend towards significance between HT and MT (Z = -1.62, p = 0.062), but no significant differences between LT and MT (Z = 0.84, p = 0.202).

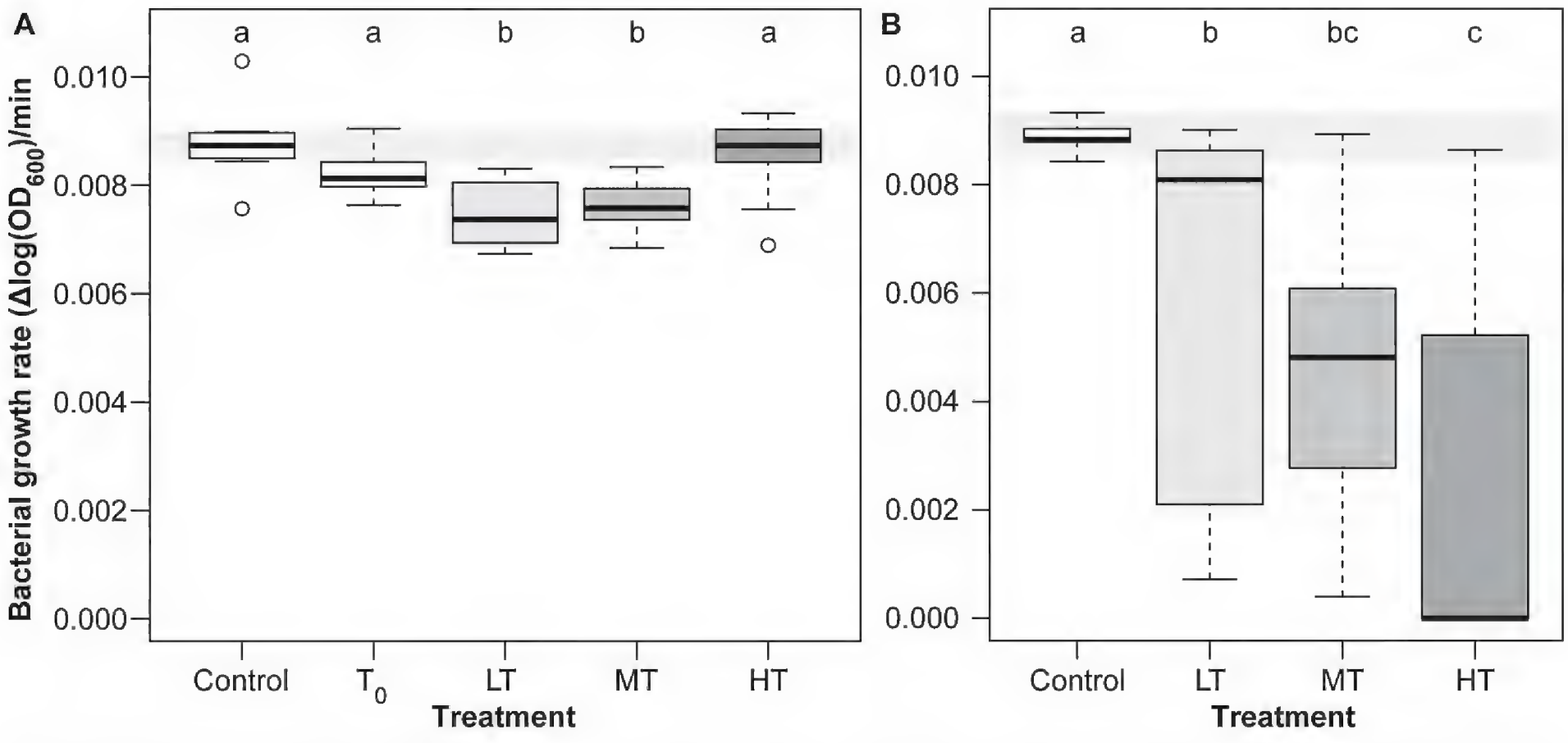

Figure 4. Constitutive **A** and total **B** immune investments (i.e. the sum of constitutive and infection-induced investments) in *M. tuberculata* as evaluated from inhibition tests that measure the *B. cereus* growth rate for standardised individual gastropod samples. Significant differences are indicated with different letters above the box plots for the various treatments. For comparison, a light grey horizontal band indicates uninhibited bacterial growth rates, i.e. those measured from positive control samples (bacteria + saline).

Our glm did not respect model assumptions, which we resolved by reverting to a simpler linear model with Gaussian distribution and this model confirmed the abovementioned results (see Suppl. material 1).

Discussion

Robustness and representativeness

Our experimental conditions were homogeneous amongst replicates, except for small, unexpected differences in conductivity due to differential evaporation and gradual enrichment of salts in aquaria MT2 and HT2 compared to others. Our osmotic water has a conductivity of ~ 30 µS/cm and, as water changes were partial, differential evaporation resulted in a gradual enrichment of salts in MT2 and HT2 over time. These differences remained small (maximum difference in median conductivity ~ 40 µS/cm) and we considered them negligible for *Melanoides tuberculata*, which occurs naturally in waters ranging from 200 to 20,000 µS/cm (Brown 1994, p. 490).

Our nine parent populations were homogeneous in shell size, with no significant differences amongst populations, treatments or replicates, indicating that our results should not be affected by size-related fecundity differences in parents. Throughout our experiment, replicates showed highly similar results, although fewer juveniles were produced compared to expectations from a preliminary experiment. For this preliminary experiment, populations were constructed as reported here, with adults of similar shell height (~ 14.5 mm), which resulted on average in ~ 16 juveniles/population/week, compared to the ~ 3 juveniles/population/week reported here. This lower numbers of juveniles increased stochasticity amongst replicates and reduced statistical power somewhat, but, given similar findings in both experiments, we consider our results robust and representative. Nevertheless, jointly, these experiments indicate substantial fluctuation in intraspecific fecundity over time, consistent with earlier reports on *M. tuberculata* (Berry and Haji Kadri 1974; Pointier et al. 1992; Facon et al. 2008) and in *Culex* mosquitoes (Ciota et al. 2014).

Life-history traits

In what follows, we compare data on life-history traits from our experiment with information from previous studies, but the presence of several deeply divergent lineages within *M. tuberculata* and the lack of phylogenetic information for organisms in most earlier studies complicate these comparisons. Indeed, life-history traits may differ amongst the deeply divergent lineages, which could lead to an overestimation of intraspecific variability by incorporating variation from lineages that actually may represent distinct species.

Fecundity was low during our experiment with ~ 0.3 juveniles per mother per week (or ~ 1.6 juveniles/mother/week during our preliminary experiment), versus 2.8–10.5 juveniles/mother/week in Facon et al. (2008) for various lineages from Martinique and 0.7–3.5 juveniles/mother/week with substantial individual variation for Malayan *M. tuberculata* (Berry and Haji Kadri 1974). Fecundity did not vary with temperature, but more juveniles were produced in the first cohort. A similar rapid release of juveniles at the onset of experiments has been observed in other *M. tuberculata* morphs/strains (Berry and Haji Kadri 1974) and may have been caused by the opportunity of encountering an empty habitat or, alternatively, by stress from

handling as observed in viviparid gastropods (Berry 1974). These viviparids displayed a temporarily accelerated release of juveniles by precocious expulsion followed by a period of reduced fecundity. We have observed similar brood-dumping in *M. tuberculata* on some occasions and it has also been observed in the paludomid genus *Lavigeria* from Lake Tanganyika (Jonathan Todd, pers. comm.), but in our experiment, *M. tuberculata* females continued releasing more juveniles also in the second week, thus for a prolonged period after potential stress related to animal handling and translocation, after which juvenile expulsion stabilised. Livshits and Fishelson (1983) indicated a negative correlation between the number of juveniles released by a population of *M. tuberculata* over time and crowding in aquaria and hypothesised a 'group effect' on the frequency with which juveniles are released, so that translocation of individuals from crowded to empty aquaria at the onset of our experiment may have triggered this burst of juvenile release. Bursts of juvenile expulsion upon translocation is a strategy that would enhance chances of population establishment in new environments.

Our juveniles had a shell height of ~ 2.6 mm upon emergence, which is similar to those of other morphs/strains of *M. tuberculata* (Berry and Haji Kadri 1974; Livshits and Fishelson 1983; Pointier 1989; Facon et al. 2008). At lower temperatures, juveniles emerged smaller and grew slower. The smaller juvenile size at birth in cold conditions could either result from faster expulsion by mothers or slower growth in the brood pouch. Given that *M. tuberculata* is an ectotherm and that we found slower growth at low temperatures both for juveniles and adults, growth in the brood pouch is likely temperature-dependent too. This inference is further corroborated by the absence of differences in fecundity: If females were to emit juveniles faster at lower temperatures, we would have expected higher fecundity in LT compared to MT and HT treatments, which was not observed.

Throughout our experiment, we observed faster growth rates in both adults and juveniles as temperatures increased, which is consistent with observations in other gastropods (Jokinen et al. 1982). Given that maturity was reached at similar sizes in all populations (at ~ 12–13 mm), differential growth implied shorter generation times in HT than in MT and even more so than in LT treatments. Generation times in HT populations were comparable to those reported by Pointier et al. (1992) and Livshits and Fishelson (1983). Our data on *M. tuberculata* did not support Bergmann's rule that maturation occurs at larger body size in cold environments nor the expectation from optimality models of sexual maturation at smaller size in cold environments. Instead, maturation occurred at similar size regardless of temperature, but with drastically different generation times. A more quantitative evaluation with better control over juvenile mortality and the proportion of juveniles that have reached sexual maturity should be undertaken before drawing further conclusions. Whereas we did not observe a direct effect of temperature on fecundity in our experiment, a trans-generational effect is expected and we also expect an effect of temperature on rates of DNA nucleotide substitutions (Gillooly et al. 2005), amongst others due to differences in metabolic rates and generation times.

In warm environments, juvenile survival was lower, at least under standardised feeding, as expected from other study systems (Taj and Jung 2012; Ciota et al. 2014), likely due to increased intraspecific competition and/or physiological stress from higher metabolic rates. Qualitatively, food was consumed faster in HT aquaria than in MT and especially compared to that in LT aquaria, which may support this hypothesis. On average, survival was lower in smaller compared to larger juveniles, as reported before (Berry and Haji Kadri 1974).

Immune responses

Temperature affected both constitutive and total immune responses after bacterial stimulation in *M. tuberculata*. Costly constitutive immunity was significantly reduced at high compared to low temperatures, whereas the total immune response after bacterial stimulation strongly increased with increasing temperatures. Assuming that, after initial acclimatisation, the constitutive immune status in F_0 parents remained stable throughout our experiment, these results suggest either strong variation in infection-induced immune responses or in the timing of those responses depending on temperature. Jointly, our results indicate that *M. tuberculata* uses compensatory immune strategies depending on environmental conditions, which confirm the EICA-refined hypothesis and would enhance competitiveness. A possible mechanism for our observations is an immune-related metabolic switch from oxidative phosphorylation, which produces more ATP, but is slow, to aerobic glycolysis, which is less energy-efficient, but faster, known as the 'Warburg Effect' (Escoll and Buchrieser 2018; Makowski et al. 2020). This switch is known to occur in response to microbial detection and/or hypoxia sensing by hypoxia-inducible factors (HIF), as intracellular dissolved oxygen is depleted during microbial proliferation (Phan and Goldrath 2015; Graham and Presnell 2017; Kim et al. 2021). By redirecting glycolysis precursors towards immune pathways, this mechanism could rebalance energy between immunity and other physiological functions (Demas et al. 2012). In our study, warmer conditions may allow *M. tuberculata* to activate immune inducible pathways before or at the onset of microbial proliferation, perhaps because infection would deplete oxygen faster as metabolic rates are higher or HIF may be more sensitive in warmer conditions, rendering infection-induced immunity responses more rapid or efficient (and costly, constitutive immunity unnecessary).

The observed eco-immunological responses suggest a delicate coupling between immune responses and individual eco-physiological state. Interestingly, we observed larger inter-individual variability in total immune responses after bacterial stimulation than in constitutive immune responses, which, as indicated above, suggests high variability in infection-induced responses. This variability resulted in some significant differences amongst replicates although these differences were substantially smaller than those amongst treatments. Therefore, we only interpret general tendencies for total immune responses after bacterial stimulation, which could be explained in two ways. First, manipulator bias could have enhanced variation in bacterial stimulation as lethal or ineffective pricks would reduce immune responses. We reduced such bias by using heat-inactivated bacteria, by making two pricks to the foot of each individual (all by the same person) and by verifying that all individuals were alive after the incubation period. In light of these precautions, a second, more likely explanation is that high variability in infection-induced immune responses represents a (potentially adaptive) population-level strategy to cope with unpredictable infection dynamics in changing (post-invasion) environments, consistent with diversified bet-hedging, i.e. enhancing variation in responses to minimise temporal fitness variation at the expense of reduced time-averaged fitness (see Childs et al. (2010)).

Effects of temperature on the invasive potential

Although proportionally larger temperature changes are predicted at mid- and high latitudes, warming will likely affect tropical ectotherms more than temperate ectotherms due to exponential increases in physiology and metabolic rates

(Dillon et al. 2010). Temperature differences affect various life-history traits in *M. tuberculata* directly or indirectly: Fecundity is not impacted directly, but growth and generation time are, which will increase fecundity at higher temperatures within physiological limits indirectly. Increased fecundity at high temperatures would not necessarily enhance total fitness, however, as juvenile survival was reduced, which suggests that selection acts on metabolic efficiency near the upper temperature limit. *Melanoides tuberculata* displays compensatory mechanisms to cope with changing/fluctuating environmental conditions: at low temperatures, growth rates and mortality are lower, whereas at high temperatures, growth rates increase, resulting in a decrease of generation times, but at the cost of increased juvenile mortality. While our experiments did not simulate natural temperature fluctuations, experimental comparisons suggest that uniform temperatures accurately represent the effects of daily mean temperature on freshwater invertebrate development (Milby and Meyer 1986). Furthermore, in large, deep lakes such as Lake Malawi/Nyassa, daily fluctuations are buffered, but seasonal temperature fluctuations may still change the invasion potential and competitive pressure of *M. tuberculata* throughout the year. Environment-mediated versatility in life-history traits could be advantageous to invaders to gain a competitive edge over native taxa.

We also observed compensatory mechanisms for immune investments of *M. tuberculata*: at higher temperatures, we observed a strong decrease in costly constitutive investments, but a stronger total immune response upon bacterial stimulation, suggesting investment in more energy-efficient induced immunity. Our observations confirm the EICA-refined hypothesis and suggest that the retained energy is, in part, redirected to growth and reproduction (by enhanced maternal investment in juvenile growth), enhancing competitiveness. At the population level, we observed large variation in total individual immune responses upon bacterial stimulation compared to constitutive responses, especially at higher temperatures. This variability may constitute an adaptive strategy in shaping efficient immune defences in unpredictable environments and/or against unknown pathogens (Prüter et al. 2020), potentially exemplifying diversified bet-hedging. Variability in induced immune responses may help reduce temporal fitness losses during translocations, environmental change and extreme climate events, but its riskier nature compared to constitutive immunity may contribute to increased juvenile mortality as temperatures increase. As diversified bet-hedging is favoured under fluctuating environmental conditions, it may act as pre-adaptation to environmental challenges encountered upon invasion, but also amid global warming. To our knowledge, our study is the first to show drastic changes in immune strategies depending on environmental conditions, providing insight into how immune strategies may contribute to invasiveness.

The observed compensatory mechanisms in life-history traits and immune responses likely give invasive *M. tuberculata* a competitive advantage in tropical and subtropical environments amid global warming. However, even in areas were *M. tuberculata* does not establish, its temporary presence could still harm native populations, especially when conditions approach the metabolic limits of these populations and/or when the invader drains resources. Such species-specific versatility, which is likely shared amongst many invasive species and the intricate interactions with multidimensional anthropogenic

stressors confound predictions of invasion dynamics and ecosystem consequences, especially at large spatiotemporal scales. Understanding such versatility is crucial for evidence-based conservation of native species (Blackburn et al. 2011), especially in combination with long-term monitoring of ecosystem change and native population dynamics to guide risk assessments (see the European Union Invasive Alien Species Regulation EU 1143/2014) and informed management strategies (McNeely et al. 2001; CBD 2020; Global Invasive Species Programme; https://www.gisp.org). Whereas the importance of considering variation in species-specific traits in case-by-case assessments of invasive species is recognised in policy, the timely construction of reliable data on how species-specific versatility contributes to invasiveness remains challenging, perhaps due to the complexity of interactions as documented here for *Melanoides tuberculata*.

Acknowledgements

We thank Jacques Verniers, Nore Praet, Wout Salenbien for help with fieldwork and Friedemann Schrenk, Harrison Simfukwe and the Cultural and Museum Centre Karonga for logistic support. Estelle-Marie Blanquart, Tony Court, Thibaut Dugay and Zakia Sultana helped with running the preliminary experiment and Sylvie Flourez with bacterial isolation. We are grateful to Jonathan Todd and two anonymous reviewers for comments that improved this work.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Our animal experiments were conducted in full compliance with applicable local and national regulations. Furthermore, our experimental facility is equipped with filtration systems to prevent the release of any propagules into the natural environment.

Funding

This project was funded by the Flanders Research Foundation, the Leopold-III fund, the Agence French Nationale de la Recherche via ANR-JCJC-EVOLINK (ANR-17-CE02-0015), the French National Centre for Scientific Research (CNRS) and the European Fund for Regional Development (FEDER) via FEDER-ERC-EVORAD. Furthermore, we thank the projects CPER-CLIMIBIO and CPER-ECRIN, which are funded by the French Ministère de l'Enseignement Supérieur et de la Recherche, the Region Hauts-de-France and the FEDER.

Author contributions

Research was conceptualised and supervised by BVB and VCH; resources were collected by BVB, GP and FDC; experiments were undertaken by JO, AYD, BVB, CMOS and RH; data on life-history traits were collected and analysed by JO, BVB, CMOS, RH and NDP; immune data were collected by JO, ACH and VCH and analysed by VCH; BVB and VCH have drafted the manuscript, with input from all authors; BVB, VCH, GP and FDC participated to project administration; BVB and VCH have acquired funding. All authors gave final approval for publication; GP, FDC and BVB communicate to policy- and decision-makers.

Author ORCIDs

Bert Van Bocxlaer https://orcid.org/0000-0003-2033-326X
Claudia M. Ortiz Sepulveda https://orcid.org/0000-0003-0072-719X
Alexis Y. Dollion https://orcid.org/0000-0003-1373-2588
Fred D. Chibwana https://orcid.org/0000-0003-0561-8849
Virginie Cuvillier-Hot https://orcid.org/0000-0002-3433-1110

Data availability

All data for this study are provided in Suppl. material 2–9.

References

Angilletta MJ (2009) Thermal adaptation - A theoretical and empirical synthesis. Oxford Univ. Press, Oxford. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Angilletta MJ, Niewiarowski PH, Dunham AE, Leaché AD, Porter WP (2004) Bergmann's Clines in Ectotherms: Illustrating a life-history perspective with sceloporine lizards. American Naturalist 164: E168–E183. https://doi.org/10.1086/425222

Antão LH, Bates AE, Blowes SA, Waldock C, Supp SR, Magurran AE, Dornelas M, Schipper AM (2020) Temperature-related biodiversity change across temperate marine and terrestrial systems. Nature Ecology & Evolution 4: 927–933. https://doi.org/10.1038/s41559-020-1185-7

Atkinson D (1994) Temperature and organism size: A biological law for ectotherms. Advances in Ecological Research 25: 1–58. https://doi.org/10.1016/S0065-2504(08)60212-3

Ben-Ami F, Heller J (2005) Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanoides tuberculata.* Journal of Evolutionary Biology 18: 138–146. https://doi.org/10.1111/j.1420-9101.2004.00791.x

Ben-Ami F, Hodgson AN (2005) Ovoviviparity and the structure of the brood pouch in *Melanoides tuberculata* (Gastropoda: Prosobranchia: Thiaridae). Journal of Morphology 263: 322–329. https://doi.org/10.1002/jmor.10307

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B, Statistical Methodology 57: 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. Oikos 70: 474–478. https://doi.org/10.2307/3545787

Berry AJ (1974) Reproductive condition in two Malayan freshwater viviparid gastropods. Journal of Zoology 174: 357–367. https://doi.org/10.1111/j.1469-7998.1974.tb03163.x

Berry AJ, Haji Kadri AB (1974) Reproduction in the Malayan freshwater cerithiacean gastropod *Melanoides tuberculata.* Journal of Zoology 172: 369–381. https://doi.org/10.1111/j.1469-7998.1974.tb04113.x

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Boots M, Best A (2018) The evolution of constitutive and induced defences to infectious disease. Proceedings of the Royal Society B: Biological Sciences 285: e20180658. https://doi.org/10.1098/rspb.2018.0658

Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Analytical Biochemistry 72: 248–254. https://doi.org/10.1016/0003-2697(76)90527-3

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9: 378–400. https://doi.org/10.32614/RJ-2017-066

Brown DS (1994) Freshwater snails of Africa and their medical importance. Taylor and Francis, London. https://doi.org/10.1201/9781482295184

CBD (2020) Global Biodiversity Outlook 5. Secretariat of the Convention on Biological Diversity, Montreal, Canada.

Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. Proceedings of the Royal Society B: Biological Sciences 277: 3055–3064. https://doi.org/10.1098/rspb.2010.0707

Ciota AT, Matachiero AC, Kilpatrick AM, Kramer LD (2014) The effect of temperature on life history traits of *Culex* mosquitoes. Journal of Medical Entomology 51: 55–62. https://doi.org/10.1603/ME13003

Cornet S, Brouat C, Diagne C, Charbonnel N (2016) Eco-immunology and bioinvasion: Revisiting the evolution of increased competitive ability hypotheses. Evolutionary Applications 9: 952–962. https://doi.org/10.1111/eva.12406

Dang VT, Speck P, Benkendorff K (2012) Influence of elevated temperatures on the immune response of abalone, *Haliotis rubra.* Fish & Shellfish Immunology 32: 732–740. https://doi.org/10.1016/j.fsi.2012.01.022

De Block M, Stoks R (2003) Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. Journal of Evolutionary Biology 16: 986–995.

Demas GE, Greives T, Chester E, French S (2012) The energetics of immunity: Mechanisms mediating trade-offs in ecoimmunology. In: Demas GE, Nelson RJ (Eds) Ecoimmunology. Oxford Univ. Press, Oxford, UK, 259-296.

Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. Nature 467: 704–707. https://doi.org/10.1038/nature09407

Dinno A (2017) dunn.test: Dunn's test of multiple comparisons using rank sums. https://CRAN.R-project.org/package=dunn.test

Donohue I, Petchey OL, Montoya JM, McNally L, Viana M, Healy K, Lurgi M, O'Connor NE, Emmerson MC (2013) On the dimensionality of ecological stability. Ecology Letters 16: 421–429. https://doi.org/10.1111/ele.12086

Dudgeon D (1986) The life cycle, population dynamics and productivity of *Melanoides tuberculata* (Müller, 1774) (Gastropoda: Prosobranchia: Thiaridae) in Hong Kong. Journal of Zoology 208: 37–53. https://doi.org/10.1111/j.1469-7998.1986.tb04707.x

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews 81: 163–182. https://doi.org/10.1017/S1464793105006950

Duggan IC (2002) First record of a wild population of the tropical snail *Melanoides tuberculata* in New Zealand natural waters. New Zealand Journal of Marine and Freshwater Research 36: 825–829. https://doi.org/10.1080/00288330.2002.9517135

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends in Ecology & Evolution 14: 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7

Escoll P, Buchrieser C (2018) Metabolic reprogramming of host cells upon bacterial infection: Why shift to a Warburg-like metabolism? The FEBS Journal 285: 2146–2160. https://doi.org/10.1111/febs.14446

Facon B, Pointier J-P, Glaubrecht M, Poux C, Jarne P, David P (2003) A molecular phylogeography approach to biological invasions of the New World by parthenogenetic thiarid snails. Molecular Ecology 12: 3027–3039. https://doi.org/10.1046/j.1365-294X.2003.01972.x

Facon B, Pointier J-P, Jarne P, Sarda V, David P (2008) High genetic variance in life-history strategies within invasive populations by way of multiple introductions. Current Biology 18: 363–367. https://doi.org/10.1016/j.cub.2008.01.063

Genner MJ, Michel E, Erpenbeck D, De Voogd N, Witte F, Pointier J-P (2004) Camouflaged invasion of Lake Malawi by an Oriental gastropod. Molecular Ecology 13: 2135–2141. https://doi.org/10.1111/j.1365-294X.2004.02222.x

Genner MJ, Todd JA, Michel E, Erpenbeck D, Jimoh A, Joyce DA, Piechocki A, Pointier J-P (2007) Amassing diversity in an ancient lake: Evolution of a morphologically diverse parthenogenetic gastropod assemblage in Lake Malawi. Molecular Ecology 16: 517–530. https://doi.org/10.1111/j.1365-294X.2006.03171.x

Gillooly JF, Allen AP, West GB, Brown JH (2005) The rate of DNA evolution: Effects of body size and temperature on the molecular clock. Proceedings of the National Academy of Sciences of the United States of America 102: 140–145. https://doi.org/10.1073/pnas.0407735101

Gissi E, Schiebinger L, Hadly EA, Crowder LB, Santoleri R, Micheli F (2023) Exploring climate-induced sex-based differences in aquatic and terrestrial ecosystems to mitigate biodiversity loss. Nature Communications 14: e4787. https://doi.org/10.1038/s41467-023-40316-8

González-Estrada E, Villaseñor-Alva JA (2020) goft: Tests of fit for some probability distributions. https://CRAN.R-project.org/package=goft

Graham AM, Presnell JS (2017) Hypoxia Inducible Factor (HIF) transcription factor family expansion, diversification, divergence and selection in eukaryotes. PLoS ONE 12: e179545. https://doi.org/10.1371/journal.pone.0179545

Graves S, Piepho H-P, Selzer L, Dorai-Raj S (2019) multcompView: Visualizations of Paired Comparisons. https://CRAN.R-project.org/package=multcompView

Hartig F (2024) DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models, https://CRAN.R-project.org/package=DHARMa

Hecky RE, Mugidde R, Ramlal PS, Talbot MR, Kling GW (2010) Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshwater Biology 55: 19–42. https://doi.org/10.1111/j.1365-2427.2009.02374.x

Heller J, Farstey V (1990) Sexual and parthenogenetic populations of the freshwater snail *Melanoides tuberculata* in Israel. Israel Journal of Zoology 37: 75–87.

Huang X, Li S, Ni P, Gao Y, Jiang B, Zhou Z, Zhan A (2017) Rapid response to changing environments during biological invasions: DNA methylation perspectives. Molecular Ecology 26: 6621–6633. https://doi.org/10.1111/mec.14382

Hulme PE (2017) Climate change and biological invasions: Evidence, expectations, and response options. Biological Reviews 92: 1297–1313. https://doi.org/10.1111/brv.12282

IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). In: Brondizio ES, Settele J, Díaz S, Ngo HT (Eds) IPBES secretariat, Bonn, Germany, 1148 pp.

Jacob J (1957) Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidy. I. Ontogenesis of the parthenogenetic species of *Melanoides* (Prosobranchia-Gastropoda). Transactions of the Royal Society of Edinburgh 63: 341–352. https://doi.org/10.1017/S0080456800009534

Jensen MP, Allen CD, Eguchi T, Bell IP, LaCasella EL, Hilton WA, Hof CAM, Dutton PH (2018) Environmental warming and feminization of one of the largest sea turtle populations in the world. Current Biology 28: 154–159. https://doi.org/10.1016/j.cub.2017.11.057

Jokinen EH, Guerette J, Kortmann RW (1982) The natural history of an ovoviviparous snail, *Viviparus georgianus* (Lea) in a soft-water eutrophic lake. Freshwater Invertebrate Biology 1: 2–17. https://doi.org/10.2307/1467137

Kamiya T, Oña L, Wertheim B, van Doorn GS (2016) Coevolutionary feedback elevates constitutive immune defence: A protein network model. BMC Evolutionary Biology 16: e92. https://doi.org/10.1186/s12862-016-0667-3

Kim C-H, Park CJ, Kim EJ, Nam YK (2021) Transcriptional modulation patterns of abalone *Haliotis discus hannai* hypoxia inducible factor-1α (HIF-1α) in interdependent crosstalk between hypoxia, infection, and environmental stresses. Aquaculture Reports 19: e100566. https://doi.org/10.1016/j.aqrep.2020.100566

Lee KA, Klasing KC (2004) A role for immunology in invasion biology. Trends in Ecology & Evolution 19: 523–529. https://doi.org/10.1016/j.tree.2004.07.012

Lenoir J, Svenning J-C (2015) Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38: 15–28. https://doi.org/10.1111/ecog.00967

Lenth RV (2025) emmeans: Estimated marginal means, aka least-squares means. https://CRAN.R-project.org/package=emmeans

Lévêque C, Dejoux C, Lauzanne L (1983) The benthic fauna: ecology, biomass and communities. In: Carmouze JP, Durand JR (Eds) Lake Chad: Ecology and productivity of a shallow tropical ecosystem. W. Junk, The Hague, 233–272. https://doi.org/10.1007/978-94-009-7266-7_9

Li Y, Qin JG, Abbott CA, Li X, Benkendorff K (2007) Synergistic impacts of heat shock and spawning on the physiology and immune health of *Crassostrea gigas*: An explanation for summer mortality in Pacific oysters. American Journal of Physiology. Regulatory, Integrative and Comparative Physiology 293: R2353–R2362. https://doi.org/10.1152/ajpregu.00463.2007

Li Y, Xue Y, Peng Z, Zhang L (2023) Immune diversity in lophotrochozoans, with a focus on recognition and effector systems. Computational and Structural Biotechnology Journal 21: 2262–2275. https://doi.org/10.1016/j.csbj.2023.03.031

Livshits G, Fishelson L (1983) Biology and reproduction of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia) in Israel. Israel Journal of Zoology 32: 21–35.

Lodge DM (1993) Biological invasions: Lessons for ecology. Trends in Ecology & Evolution 8: 133–137. https://doi.org/10.1016/0169-5347(93)90025-K

Madsen H (1992) Food selection by freshwater snails in the Gezira irrigation canals, Sudan. Hydrobiologia 228: 203–217. https://doi.org/10.1007/BF00006587

Makowski L, Chaib M, Rathmell JC (2020) Immunometabolism: From basic mechanisms to translation. Immunological Reviews 295: 5–14. https://doi.org/10.1111/imr.12858

Mayhew PJ, Bell MA, Benton TG, McGowan AJ (2012) Biodiversity tracks temperature over time. Proceedings of the National Academy of Sciences of the United States of America 109: 15141–15145. https://doi.org/10.1073/pnas.1200844109

McNeely JA, Mooney HA, Neville LE, Schel P, Waage JK (2001) A global strategy on invasive alien species. IUCN, Gland, Switzerland; Cambridge, UK.

Milby MM, Meyer RP (1986) The influence of constant versus fluctuating water temperatures on the preimaginal development of *Culex tarsalis.* Journal of the American Mosquito Control Association 2: 7–10.

Mitchell AJ, Brandt TM (2005) Temperature tolerance of red-rim melania *Melanoides tuberculatus*, an exotic aquatic snail established in the United States. Transactions of the American Fisheries Society 134: 126–131. https://doi.org/10.1577/FT03-178.1

Okumura DT, Rocha O (2020) Life history traits of the exotic freshwater snail *Melanoides tuberculata* Müller, 1774 (Gastropoda, Thiaridae), and its sensitivity to common stressors in freshwaters. Acta Limnologica Brasiliensia 32: e19. https://doi.org/10.1590/s2179-975x0819

Oscoz J, Tomás P, Durán C (2010) Review and new records of non-indigenous freshwater invertebrates in the Ebro River basin (Northeast Spain). Aquatic Invasions 5: 263–284. https://doi.org/10.3391/ai.2010.5.3.04

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends in Ecology & Evolution 24: 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Phan AT, Goldrath AW (2015) Hypoxia-inducible factors regulate T cell metabolism and function. Molecular Immunology 68: 527–535. https://doi.org/10.1016/j.molimm.2015.08.004

Pinzón JH, Dornberger L, Beach-Letendre J, Weil E, Mydlarz LD (2014) The link between immunity and life history traits in scleractinian corals. PeerJ 2: e628. https://doi.org/10.7717/peerj.628

Pointier J-P (1989) Conchological studies of *Thiara* (*Melanoides*) *tuberculata* (Mollusca: Gastropoda: Thiaridae) in the French West Indies. Walkerana 3: 203–209.

Pointier J-P (2001) Invading freshwater snails and biological control in Martinique island, French West Indies. Memorias do Instituto Oswaldo Cruz 96: 67–74. https://doi.org/10.1590/S0074-02762001000900009

Pointier J-P, Delay B, Toffart JL, Lefèvre M, Romero-Alvarez R (1992) Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. Journal of Molluscan Studies 58: 415–423. https://doi.org/10.1093/mollus/58.4.415

Prüter H, Franz M, Twietmeyer S, Böhm N, Middendorff G, Portas R, Melzheimer J, Kolberg H, von Samson-Himmelstjerna G, Greenwood AD, Lüschow D, Mühldorfer K, Czirják GÁ (2020) Increased immune marker variance in a population of invasive birds. Scientific Reports 10: e21764. https://doi.org/10.1038/s41598-020-78427-7

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rader RB, Belk MC, Keleher MJ (2003) The introduction of an invasive snail (*Melanoides tuberculata*) to spring ecosystems in the Bonneville Basin, Utah. Journal of Freshwater Ecology 18: 647–657. https://doi.org/10.1080/02705060.2003.9664007

Sala OE, Chapin FSI, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413: 591–596. https://doi.org/10.1038/35098000

Schmid-Hempel P, Ebert D (2003) On the evolutionary ecology of specific immune defence. Trends in Ecology & Evolution 18: 27–32. https://doi.org/10.1016/S0169-5347(02)00013-7

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671–675. https://doi.org/10.1038/nmeth.2089

Sponaugle S, Grorud-Colvert K, Pinkard D (2006) Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. Marine Ecology Progress Series 308: 1–15. https://doi.org/10.3354/meps308001

Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. Evolution 40: 893–913. https://doi.org/10.1111/j.1558-5646.1986.tb00560.x

Strayer DL (2010) Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Szuwalski CS, Aydin K, Fedewa EJ, Garber-Yonts B, Litzow MA (2023) The collapse of eastern Bering Sea snow crab. Science 382: 306–310. https://doi.org/10.1126/science.adf6035

Taj HFE, Jung C (2012) Effect of temperature on the life-history traits of *Neoseiulus californicus* (Acari: Phytoseiidae) fed on *Panonychus ulmi*. Experimental & Applied Acarology 56: 247–260. https://doi.org/10.1007/s10493-012-9516-2

Tickner D, Opperman JJ, Abell R, Acreman M, Arthington AH, Bunn SE, Cooke SJ, Dalton J, Darwall W, Edwards G, Harrison I, Hughes K, Jones T, Leclère D, Lynch AJ, Leonard P, McClain ME, Muruven D, Olden JD, Ormerod SJ, Robinson J, Tharme RE, Thieme M, Tockner K, Wright M, Young L (2020) Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. BioScience 70: 330–342. https://doi.org/10.1093/biosci/biaa002

Tolley-Jordan LR, Chadwick MA, Triplett JK (2023) DNA barcoding indicates multiple invasions of the freshwater snail *Melanoides tuberculata* sensu lato in Florida. PLoS ONE 18: e0292164. https://doi.org/10.1371/journal.pone.0292164

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421: 628–630. https://doi.org/10.1038/nature01346

Travers M-A, Basuyaux O, Le Goïc N, Huchette S, Nicolas J-L, Koken M, Paillard C (2009) Influence of temperature and spawning effort on *Haliotis tuberculata* mortalities caused by *Vibrio harveyi*: An example of emerging vibriosis linked to global warming. Global Change Biology 15: 1365–1376. https://doi.org/10.1111/j.1365-2486.2008.01764.x

Van Bocxlaer B, Albrecht C (2015) Ecosystem change and establishment of an invasive snail alter gastropod communities in long-lived Lake Malawi. Hydrobiologia 744: 307–316. https://doi.org/10.1007/s10750-014-2093-0

Van Bocxlaer B, Clewing C, Mongindo Etimosundja J-P, Kankonda A, Wembo Ndeo O, Albrecht C (2015) Recurrent camouflaged invasions and dispersal of an Asian freshwater gastropod in tropical Africa. BMC Evolutionary Biology 15: e33. https://doi.org/10.1186/s12862-015-0296-2

Wang H-Y, Shen S-F, Chen Y-S, Kiang Y-K, Heino M (2020) Life histories determine divergent population trends for fishes under climate warming. Nature Communications 11: e4088. https://doi.org/10.1038/s41467-020-17937-4

Weiskopf SR, Rubenstein MA, Crozier LG, Gaichas S, Griffis R, Halofsky JE, Hyde KJW, Morelli TL, Morisette JT, Muñoz RC, Pershing AJ, Peterson DL, Poudel R, Staudinger MD, Sutton-Grier AE, Thompson L, Vose J, Weltzin JF, Whyte KP (2020) Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Science of the Total Environment 733: e137782. https://doi.org/10.1016/j.scitotenv.2020.137782

Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: Challenges for predicting invasive potential. Diversity & Distributions 14: 569–580. https://doi.org/10.1111/j.1472-4642.2008.00473.x

Supplementary material 1

Additional information on our experiment

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: docx

Explanation note: Additional information on bacterial isolation, selection and characterisation, on antibacterial tests, as well as additional results on statistical tests and on environmental conditions during the experiment (fig. S1).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl1

Supplementary material 2

Biweekly measured environmental conditions

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Data file on biweekly measured environmental conditions for the first 6.5 weeks of the experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl2

Supplementary material 3

Parental shell length

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Individual measurement data on the shell length of F_0 parents (in mm) at the onset of our experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl3

Supplementary material 4

Parental growth

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Individual growth measurements (in mm) of F_0 parents over the first 6.5 weeks of our experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl4

Supplementary material 5

Population-level fecundity

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Population-level fecundity data for the first six cohorts of F_1 offspring produced in our experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl5

Supplementary material 6

Measured shell length of offspring

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Individual measurement data on the shell length of F_1 offspring (in mm) at birth for the first six cohorts in our experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl6

Supplementary material 7

Offspring growth

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Individual measurement data on growth of F_1 offspring (in mm) over two-week periods.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl7

Supplementary material 8

Offspring mortality

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Population-level mortality data for the first six cohorts of F_1 offspring in our experiment expressed as the percentage death rate over the first 6.5 weeks of our experiment.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl8

Supplementary material 9

Immunological data

Authors: Bert Van Bocxlaer, Julie Offerle, Claudia M. Ortiz Sepulveda, Rémi Habert, Anne-Catherine Holl, Nicolas Denize-Proust, Alexis Y. Dollion, Grant Pawindo, Fred D. Chibwana, Virginie Cuvillier-Hot

Data type: txt

Explanation note: Bacterial growth rates as reflected by *r*-values for individual samples relating to constitutive immune responses (46j-NP-100 µg) for positive controls, T_0 individuals and our F_0 parents as well as to total immune responses (9 m-P-150 µg) for positive controls and our other five F_0 parents per experimental population.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.99.143667.suppl9